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Ecology of Enchytraeidae (Oligochaeta) in Canadian Rocky Mountain Soils

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With 2 figures

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1. Introduction

The Enchytraeidae are small oligochaetes which are known to reach high densities in a number of European localities. Their role in litter breakdown and soil formation is not thoroughly understood although their importance as secondary decomposers would appear to be considerable in mor-type soils.

DASH and CRAGG (1972) have shown that enchytraeids select plant remains rich in fungal materials and that enchytraeids showed a preference for fungi belonging to the Sphaeropsidales and to the genus *Cladosporium*.

Few data are available on their occurrence and population biology in North America and no quantitative studies have been made in Rocky Mountain habitats. This paper provides a comparative description of the ecology of enchytraeids for two sites in the Kananaskis valley, Alberta .Ten species of Enchytraeidae, belonging to seven genera have been found in the area; except *Henlea nasuta* EISEN all are new records for Canada and are described in DASH (1970).

This study was made at the Environmental Sciences Centre (University of Calgary), 50 miles west of Calgary within the Kananaskis research forest, 23 sq m*l* in area, which lies on the east slope of the Rockies.

Two sampling sites, one in aspen woodland and the other in a fen were selected for the investigations.

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2. Study areas

2.0. Aspen woodland

The aspen woodland was on the southeast slope of Pigeon Mountain altitude 1380 m (4600 ft). In addition to Aspen (*Populus tremuloides*) other tree species were *Populus tacamahacca* Mill. (= *P. balsamifera* L.), *Salix* sp., *Picea* sp., *Abies* sp., *Pinus* sp. The actual study plot contained ten living and three dead aspen trees (*Populus tremuloides*) and three willows (*Salix* sp.). The thick ground flora was dominated by various grasses and herbs which included *Rosa* sp., *Castilleja* sp., *Epilobium* sp., *Campanula* sp. and others. The soils are calcareous in origin and were of *p*H 6.4–6.7. Description of soil profile: [A_0L] 0–2 cm. Distinct litter of aspen leaves, leaf bases, grasses, form compact layer. [A_0F] 2–3 cm. Smaller litter fragments with faecal pellets; not clearly separated from A_0L. [A_0H], 3–6 (7) cm. Dark grey, dry, finely divided organic material with occasional litter fragments, root-stocks and upper part normally with faecal pellets. [A], 6 (7)–15 cm, and below. Greyish-yellow or greyish-brown, dry, upper layers crumbly; abundant smaller and larger roots with stones.

2.1. The fen

The fen is seven miles south of the research station at 1380 m (4600 ft.) It is below the northwest slope of a mountain and adjacent to a deserted beaver pond. The vegetation of the surrounding area was dominated by *Populus tremuloides* and Birch (*Betula* sp.). The study plot included four *Pinus* sp. and three spruce (*Picea* sp.).

The ground carried a thick layer of mosses (*Campylium* sp., *Tomenthypnum* sp., *Sphagnum* sp.) under Birch (*Betula* sp.). In summer *Epilobium* sp. and grasses were common. The litter and soil, *p*H 6.4. Description of soil profile: [A_0L], 0–3 cm. Moss cover; distinct litter of birch leaves, occasional aspen leaves, pine and spruce needles, grasses, form compact layer. [A_0F], 3–4 cm. Smaller litter fragments and lower part with black or greyish-black organic matter; not clearly separated from A_0L [A_0H] 4–6 cm. Greyish-black or black finely divided organic matter or very small fragments, fine roots and larger Betula roots, always waterlogged. [A_0H/A], 6–7 cm. Greyish-black or black, mixture of humus, sand, clay and Betula roots, waterlogged. [A], 7–15 cm. Greyish-black or black, sand, clay and Betula roots, waterlogged.

The fen site differed from the aspen site as follows: (**1**) It faced northwest and was permanently moist whereas the aspen site was on a southeast slope and was very dry in summer. (**2**) The fen was open whereas the aspen site was not open. (**3**) The fen, unlike the aspen site, froze early (late October or early November) and the soil remained frozen under deep cover of snow (about ½–1 m deep) until April. Ice crystals occurred in samples taken in early May.

2.2. Climate

The Kananaskis valley with its wide range of altitude shows considerable fluctuations in climate. It has a short dry summer and a long cold winter with intermittent warm Chinook winds. About 50% of the precipitation falls as snow. Annual precipitation in the area was 514 mm in 1967, 685 mm in 1968 and 554 mm in 1969 and the mean air temperature in the area was 2.60 °C in 1967 and in 1968 and 2.25 °C in 1969. Table 1 gives the soil moisture of the study areas.

In winter, snow may be 60–90 cm (2–3 ft) deep and may lie from October to April. The ground remains frozen from late November to March in the aspen woodland and from early November to mid April in the fen. At 1–3 cm depth, winter soil temperatures in both study sites were below zero and in summer, they could be as high as 25 °C.

Table 1 Mean humidity index* of soil (0–6 cm) from June 1968 to November 1969

Season	Site	
	Aspen woodland	Fen
Spring (March–May)	2.45	9.00
Summer (June–August)	0.59	3.60
Autumn (September–November)	1.15	4.50
Winter (December–February)	2.13	9.00

*) The humidity index is the ratio of the weight of water to the dry weight of soil (BANAGE 1966)

3. Sampling and extraction techniques

Two sampling plots each 12×12 m were marked out, one in each site. Their selection was based on a visual assessment of the areas. Each plot was divided into 36 subplots (each 2×2 m). Fifteen pairs of litter and soil cores of size 9.6 cm² surface area and 9 cm deep were taken monthly using a sampler lined with tufnol rings (each 3 cm deep and 3 cm diam.). Few enchytraeids occurred below 9 cm and routine sampling was therefore confined to the top 9 cm of the profile. The position of the paired samples was obtained by using random numbers (SNEDECOR and COCHRAN 1967). The samples were collected by stratified random sampling methods to avoid bias. Fifteen samples had a standard error of the mean of 15–20% whereas for thirty samples the value was 10%. This figure did not differ significantly from that obtained for forty-five samples and therefore the monthly unit was fixed at thirty samples.

An additional five cores were taken each sampling period for water content determinations (see Table 1). During the summer, samples were taken from other parts of the aspen woodland for comparison with the study plot and they showed no significant differences from the study plot.

The tufnol rings containing the soil cores were slipped out of the sampler into polythene bags and taken to the laboratory where they were subdivided into layers each 1.5 cm deep. When extraction could not be performed immediately on return to the laboratory, the bags containing the cores were stored at 5 °C.

The worms were extracted using the wet funnel extraction method (O'CONNOR 1955). After extraction they were separated into species and into three different age classes, namely: juveniles ($\leq$ 2 mm); nonmature ($>$ 2 mm but lacking spermathecae); adults. Each age class was counted separately.

4. Occurrence of Enchytraeidae in the Kananaskis Region

4.0. Qualitative distribution

In addition to the monthly samples for the estimation of seasonal fluctuations in density in the two main sites, samples were taken from coniferous forest soils (2–5 miles south of the research station) to determine species composition. Table 2 shows the qualitative distribution of the different species of Enchytraeidae in the Kananaskis valley. The aspen site was dominated by the genera *Marionina* and *Henlea* and the fen site by the genera *Marionina* and *Cernosvitoviella*.

4.1. Microdistribution

4.1.1. Non normal distribution

Sample unit values were grouped into frequency distributions around their individual means with multiples of standard deviations as class boundaries and compared with a

Table 2 Qualitative distribution of Enchytraeidae in the study areas of the Kananaskis Valley

Species	Aspen area	Coniferous area	Fen area
Henlea perpusilla NIELSEN and CHRISTENSEN 1959	+	+	+
Henlea nasuta EISEN 1878	+	+	—
Marionina canadensis DASH 1970	+	+	+
Marionina craggi DASH 1970	+	+	+
Marionina argentea MICHAELSEN 1889	—	—	+
Enchytraeus buchholzi VEJDOVSKY 1879	+	+	+
Fridericia bulboides NIELSEN and CHRISTENSEN 1959	+	+	+
Černosvitoviella christenseni DASH 1970	—	—	+
Mesenchytraeus armatus kananaskis DASH 1970	—	—	+
Bryodrilus parvus kananaskis DASH 1970	+	+	+

normal distribution. In all cases, the distribution as skewed with an excess of negative deviates and few large positive deviates. Random sample data statistics for skew (g_1) and kurtosis (g_2), (SNEDECOR and COCHRAN 1967) were applied (see Table 3). The positive values of g_1 indicate an excess of below mean values and the negative values of g_2 indicate an excess of near mean values.

4.1.2. Non random distribution

Table 4 shows that in most cases the coefficient of dispersion or ratio of variance to mean (SALT and HOLLICK 1946) were above unity which indicates that the enchytraeids were aggregated.

4.2. Vertical distribution

4.2.0. Downward migration

Studies of the vertical distribution of Enchytraeidae have been made by NIELSEN (1955 a) in Denmark, O'CONNOR (1957) in North Wales, PEACHEY (1963) and SPRINGETT et al. (1970) in England and NURMINEN (1967) in Finland.

In all the above studies over 75% of the enchytraeids occurred in the top 6 cm of the soil profile. A similar distribution holds for the two sites at Kananaskis (see Table 5) with a higher percentage occurring in the 3–6 cm during the winter months.

Table 3 Values of the statistics for skew and kurtosis at Kananaskis, 1968–1969

	Skewness g_1 Aspen site	Fen site	Kurtosis g_2 Aspen site	Fen site
Summer	+1.52	+1.83	−2.70	−2.995
(June–August)	+1.52	+1.55	−3.55	−2.24
	+1.36	+1.38	−3.39	−3.35
Autumn	+1.16	+1.64	−4.19	−1.71
(August–November)	+1.20	+1.21	−4.20	−4.15
	+1.38	+1.54	−3.42	−2.95
Winter	+1.67		−2.18	
(December–February)	+1.81	+1.45	−0.87	−3.42
	+1.58		−2.71	
Spring	+1.33	+2.09	−3.90	0.27
(March–May)	+1.30	+1.71	−3.87	−1.76
	+2.03	+2.28	−5.08	2.52

Table 4 Coefficient of dispersion for total populations of enchytraeids for the sampling sites from 1968–1969

	Summer	Autumn	Winter	Spring	Summer	Autumn
Aspen site	0.93	3.00	1.35	1.25	9.44	1.75
	1.13	3.12	1.66	2.65	6.05	2.65
	1.68	1.13	0.66	3.83	7.13	5.56
Fen site	3.82	3.54	—	2.44	3.02	4.04
	2.71	2.24	1.31	2.44	4.15	6.52
	3.27	3.21	—	4.60	5.98	3.45

Table 5 Percent total Enchytraeidae extracted from different levels in the soil profile (June 1968–November 1969)

Site	Depth in cm					Total no. extracted
	0–1.5	1.5–3	3–4.5	4.5–6	6–9	
Aspen woodland						
Average	34	36	20	9	1	5244
Warm period (April–November)	36	36	18	9	1	4835
Cold period (December–March)	15	41	38	6	1	409
Fen						
Average	43	36	15	5	1	2645
Warm period (May–October)	46	36	13	4	1	2235
Cold period (November–April)	24	41	28	6	1	410

Nielsen (1955 b) recognized a slight movement downward during drought conditions and Peachey (1963) showed this to be the case for one of his sites when subjected to drying conditions. O'Connor (1957) although noticing an increase in the percentage of enchytraeids found in the deeper layers of his site under drought conditions, attributed it to differential mortality and not to downward migration. Springett et al. (1970) have now shown that rapid vertical migrations may occur in response to changes in soil moisture.

4.2.1. Diurnal movement

Samples were taken in the aspen site at 6–8 hr intervals throughout 2–3 days on each of four occasions (May, June, July, August, 1969), during periods of dry warm weather. The technique was not sufficiently sensitive to establish that movements occurred during diurnal periods but comparisons of the distribution of enchytraeids with depth, at monthly intervals, indicated significant differences in distribution between the 0–3 cm layer and the 2–6 cm layer during periods of drought in the aspen site.

4.2.2. Vertical movements in response to drying

Laboratory experiments were designed to test the effect of drying the litter surface on the vertical distribution of enchytraeids. The experimental and control material was collected from an area 90×60 cm in the aspen site. Control samples were taken from one half of the area and the other half (45×30 cm) was removed in one piece and given heat treatment in the laboratory. These experiments were repeated on five occasions.

The distribution of enchytraeids before heat treatment was determined from five cores, 9 cm deep, each cut into six layers 1.5 cm thick. Three similarly treated samples were used to determine variations in the index of humidity with depth.

The soil block was dried under an electric fan for 8 hr (4 hr treatment produced no change in the distribution of enchytraeids). Eight cores were then removed from the block and treated in a similar manner to the control samples. Five were used for the estimation of numbers of enchytraeids and three for the determination of humidity index.

Table 6 shows that the number of enchytraeids in the top 1.5 cm fell by 6 to 18% when the index of humidity dropped by 0.48 to 0.80. This fall in numbers was compensated by a corresponding rise in numbers in the 1.5—3.0 cm zone, thus demonstrating that a downward movement had taken place.

4.3. Seasonal variations in numbers

4.3.0. General distribution

When comparing results for the Kananaskis area with others obtained elsewhere, attention must be given to regional differences in climate. The Kananaskis area differs from the others in possessing a continental climate with a hot summer and a long cold winter.

The fen populations were dominated by species belonging to the genera *Marionina* and *Cernosvitoviella*. Two generations per year were only recorded for *Marionina canadensis* and *M. argentea*. A few juveniles of *Henlea perpusilla* were present in late summer — early autumn which suggests that some individuals showed a second breeding period.

The aspen site population was dominated by the genera *Henlea* and *Marionina* and most of the species present in the site showed two generations per year.

Seasonal variations for both sites are shown in fig. 1 and 2.

4.3.1 The fen site

The fen which experienced a longer winter period than the aspen site, remained waterlogged throughout the year. Thus, temperature and not moisture content must have been the main factor influencing cocoon formation, cocoon hatching, movement of enchytraeids and fluctuations in density. Soil temperature and numbers of enchytraeids showed a

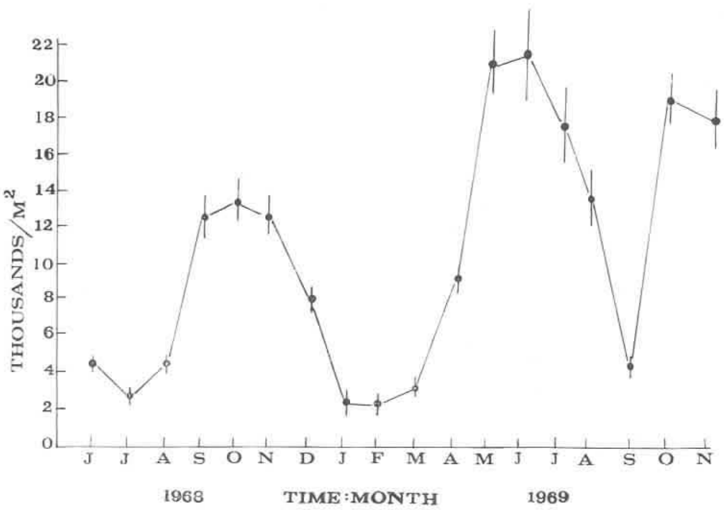

Figure 1 Seasonal variation in total numbers of Enchytraeidae in the aspen woodland site.

Table 6 Effect of drying on the distribution of Enchytraeidae in top 9 cm of profile aspen forest soil (litter + soil)

	Depth in cm										
	Humidity index of soil					Distribution of Enchytraeidae*)					
Date (1969)	0–1.5	1.5–3	3–4.5	4.5–6	6–9	0–1.5	1.5–3	3–4.5	4.5–6	6–9	Total no.
21 May											
U	2.29	1.70	1.00	0.56	0.22	57	14	16	9	4	106
Fd	1.56	1.48	1.00	0.52	0.20	49	24	15	10	2	85
29 May											
U	2.24	2.36	1.00	0.37	0.20	56	30	9	4	1	80
Fd	1.44	2.11	0.91	0.37	0.20	38	26	20	16		93
13 June											
U	1.74	2.29	1.10	0.75	0.38	36	27	20	12	5	81
Fd	1.26	1.93	1.00	0.70	0.37	30	37	18	13	2	100
2 July											
U	2.44	2.06	1.00	0.37	0.35	45	31	16	7	1	75
Fd	1.64	1.91	0.91	0.37	0.35	36	39	18	7		84
18 July											
U	1.59	1.29	0.72	0.30		68	22	7	3		60
Fd	1.10	1.00	0.79	0.35		52	32	14	2		71

Note – U = Untreated, Fd = Fan dried
*) Percent of total numbers

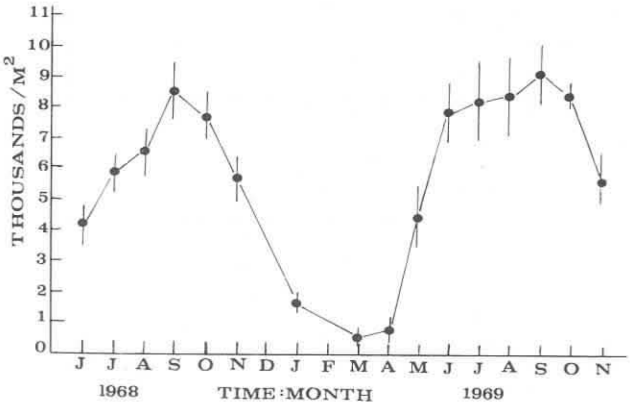

Figure 2. Seasonal variation in total numbers of Enchytraeidae in the fen.

significant, positive correlation ($r = 0.72$; 5% level), whereas moisture and numbers were not correlated for that site.

In winter the enchytraeid population was dominated by nonmature forms, in May—June by juveniles, and by June—July it was again dominated by nonmature worms. The peak density (fig. 1 and 2) was reached in August—September and numbers then gradually decreased to a minimum in winter (January).

4.3.2. The aspen site

The aspen site was subjected to prolonged dry periods and both temperature and moisture showed significant correlations with numbers of enchytraeids.

The index of humidity for May—November, showed positive correlation ($r = 0.55$) with enchytraeid numbers (5% level), thus indicating the importance of moisture for survival and growth of the population. For the same period soil temperature at 1—3 cm was positively correlated with enchytraeid numbers ($r = 0.26$).

The winter population was dominated by nonmature and mature enchytraeids. With rising soil temperatures in April—May, the proportion of juveniles (≤ 2 mm long) increased rapidly, an indication that cocoons which had overwintered had started to hatch. The populations reached a maximum in late spring (late May). The April—early June population consisted mainly of juveniles and nonmature worms. The proportion of nonmature and mature worms markedly increased in July—August with a maximum of four per cent juveniles in July 1968 and 1969.

The minimum summer densities in both 1968 and 1969 were associated with drought conditions. When the soil moisture content increased after rain in autumn (September — October), cocoons laid in spring and summer hatched and there was an immediate increase in the numbers of Enchytraeidae. Numbers gradually declined through the winter to reach their lowest level in January—February.

The following generalizations on the number of enchytraeids in different seasons in relation to soil temperature and moisture can be made: (**1**) Average soil temperature below 0 °C: This category covers periods when the soil was frozen and temperature conditions in the soil were uniform. The index of humidity was high (1.76—2.46) with the moisture present as ice. This situation occurred mainly from December to March. Throughout this period there was a gradual decrease in numbers and the density never exceeded 5000/m². (**2**) Soil temperature to 15 °C with a high humidity index. These conditions occurred at the onset of spring and continued into summer to recur in autumn. The

humidity index varied 0.61–3.68. Numbers of enchytraeids were well above 5000 (range 8000–21000/m^2). (**3**) Soil temperature 10 to 15 °C with a low humidity index. These conditions occurred in drought periods (June–July, 1968 and August–September, 1969), when the humidity index was < 0.5. Low densities below 5000/m^2 prevailed.

4.4. Biomass and production

In each month, two or three sets of 4–10 individuals of the different age classes of each species were weighed (± 0.02 mg) to estimate biomass. These determinations were then used to calculate the total biomass of each species in the monthly samples. Dry weight biomass was determined by drying the samples at 85 °C for approximately one hr. *Henlea nasuta* with 75–80% water content differed from the other species whose values lay in the 80–85% range.

Fig. 1 shows that in 1969 there were two main periods of production in the aspen site, from March to July and from September to November. The biomass changes recorded during these periods can be obtained from table 7. From March to July there was a net increase of 5.3 g/m^2 and September to November showed an increase of 1.3 g/m^2; making

Table 7 Wet weight (mg/m^2) of Enchytraeidae from aspen site (Mean $\pm$ S.E.)

1968–1969	*Henlea nasuta*	*Henlea perpusilla*	*Marionina canadensis*	*Enchytraeus buchholzi*	Others	Total
June	**1243**	**125**	**61**	**21**		**1450**
	±190	±2	±1	±2		±195
July	**840**	**182**	**29**	**7**		**1058**
	±15	±1	±1	±1		±18
August	**1035**	**242**	**50**	**31**	**19**	**1377**
	±3	±4	±1	±1	±1	±10
September	**1846**	**209**	**116**	**87**		**2258**
	±40	±10	±2	±1		±53
October	**2876**	**343**	**139**	**127**	**41**	**3526**
	±82	±46	±5	±5	±2	±140
November	**3824**	**416**	**153**	**141**	**67**	**4601**
	±172	±8	±6	±15	±1	±202
December	**1590**	**264**	**150**	**159**	**26**	**2189**
	±114	±14	±20	±16	±1	±165
January	**610**	**109**	**31**	**10**		**760**
	±10	±1	±1	±1		±13
February	**664**	**63**	**22**	**4**		**753**
	±59	±1	±1	±1		±62
March	**798**	**66**	**34**	**4**		**902**
	±6	±5	±1	±1		±13
April	**1194**	**123**	**77**	**10**		**1404**
	±58	±11	±1	±1		±71
May	**2075**	**378**	**258**	**24**	**5**	**2740**
	±77	±47	±9	±1	±1	±136
June	**4100**	594	**344**	**49**	**124**	**5211**
	±288	±43	±14	±2	±5	±352
July	**4838**	**742**	**255**	**109**	**280**	**6224**
	±264	±52	±32	±4	±10	±362
August	**3511**	**703**	**193**	**106**	**446**	**4959**
	±364	±99	±20	±9	±8	±500
September	**2158**	**145**	**32**	**12**	**313**	**2660**
	±149	±10	±1	±2	±9	±171
October	**2475**	**446**	**225**	**13**	**234**	**3443**
	±409	±38	±1	±1	±5	±454
November	**3082**	**402**	**228**	**28**	**229**	**3969**
	±234	±34	±1	±1	±6	±276

a total recorded production of 6.6 g/m² (wet weight) of new enchytraeid material. Over the period December 1968 to November 1969, the average monthly standing crop was approximately 3 g/m². Thus the recorded production was 2× the average standing crop. In 1968 the second production phase started in July and by November 3.5 g/m² had been recorded, about 3× the amount recorded in that phase in 1969.

The above calculations do not include weight losses caused by cocoon production, death of worms and stages missed in extraction. They are underestimates of actual production which must exceed by several times, the turn-over figure of 3× the average monthly biomass.

5. Discussion

Table 8 lists population densities for a range of sites. The densities at Kananaskis which experiences a continental type climate are only one tenth of the values obtained by O'Connor (1957) from coniferous forest soils in North Wales. They are, however, approximately the same as those recorded by Nurminen (1967) from Finnish coniferous forest sites which also experience a continental climate.

Nielsen (1955a, b), O'Connor (1957), Peachey (1963), Springett (1970), found one peak density in late summer or autumn and one low density period in late winter. Nurminen (1967) found two periods of high density in spring and autumn with two periods of low density in summer and winter in Finland. The population trend at Kananaskis accords with the population trend found in Finland. The minor differences between results for Finland (Nurminen 1967) and for Kananaskis can be attributed to the difference in altitude of the two sites.

The number of enchytraeids in the permanently moist fen site at Kananaskis is low when compared with the results obtained by Peachey (1963) and Springett (1970) for permanent moist habitats at Moor House, England. The Kananaskis and English moorland sites are characterized by a single high density peak in late summer and a single low density peak in winter.

The biomass values for the Kananaskis sites are lower than those recorded where (Table 8). They can be accounted for by the occurrence of low densities dominated by species of small size. The largest species *Henlea nasuta*, which was confined to the aspen site accounted for 70–90% of the total biomass of the enchytraeids found in that site.

A very tentative estimate can be made of the enchytraeid contribution to the total biomass of the microfauna in the aspen study site at Kananaskis using the frequency of occurrence of different members of the soil fauna on fungal baits (Dash and Cragg 1972). The Collembola and mites constituted about 61% and the enchytraeids about

Table 8 Number and biomass of Enchytraeidae in different habitats

Author & Region	Site	Nos. 10³/m² (Range)	Biomass (g)/M² (Annual mean)
Nielson (Denmark)	Sandy permanent Pasture		
	Stn. 1	44*	2.97
	4	30*	3.03
	18	74*	10.50
O'Connor (North Wales)	Coniferous wood	134.3*	10.79
Peachey (Pennine Moorland)	Alluvial grassland	10–25	15
	Juncus moor	130–290	53
	Nardus grassland	37–200	35
	Eroded peat	12–50	10
Dash & Cragg (Alberta)	Aspen woodland	2–22	3.00
	Fen	0.5–10	0.5

* Annual mean

3.5% of the total number of animals collected, the remainder were mainly nematodes and in all probability were underestimated. Using weights of Collembola and mites given in HALE (1966) and BERTHET (1963), the wet weight of all Collembola and mites collected from fungal baits would amount to about 40 mg which equalled the wet weight of the enchytraeids collected from the same baits.

If it is assumed that the catches in the fungal traps are representative of the relative abundance of the main groups of the microfauna, then it follows that an average monthly biomass of 3 g/m² of enchytraeids will be associated with an equal weight of Collembola and mites. Thus unless some other group of soil organisms, as yet undetected, is abundant, the maximum monthly average biomass of microfauna is unlikely to exceed 8—12 g/m² (wet wt). This estimate is low compared with the 78 g/m² (excluding Tipulidae = 56.3g/m²) found in wet *Juncus* moor in England (Moor House) where enchytraeids constituted 68% of the total biomass (CRAGG 1961).

Although the role of enchytraeids in the decomposer system is not fully understood, it is clear from various sources that many terrestrial species ingest plant remains with a high microbial and microfungal content. Furthermore, DASH & CRAGG (1972), have shown that some of the species at Kananaskis select certain fungal species. According to ZACHARIAE (1964), enchytraeid faeces play an important part in soil formation and it appears from his publications that this function of enchytraeids has been underestimated some soil types.

Information on the metabolic activity of enchytraeids is negligible, even for sites where they are the dominant members of the soil fauna. MACFADYEN (1963) has compared the animal biomass and metabolism of nine soil habitats which included mull and mor forest soils and estimated that in general, the soil fauna released between 10 and 20% of the total energy input of the habitat. In his estimates, the mor sites, which included coniferous forest showed a high metabolic output on the part of small decomposers which comprised Collembola, nematodes, enchytraeids and oribatid mites, where they compensated for the absence of large decomposers. O'CONNOR (1967), has calculated that the respiratory activity, of enchytraeids (average monthly biomass 10.8 g/m² wet wt) in a Douglas fir plantation in North Wales, accounted for 11% of the total annual energy input to the forest floor (1350 Kcal/m²). This estimate takes no account of the energy consumed in growth and reproduction. Thus the total metabolic activity is likely to exceed the estimate by at least 20% if the values given by ENGELMANN (1961) for oribatid mite populations can be taken as a guide.

The annual litter input to the aspen site at Kananaskis was high, consisting of 300 g (dry wt)/m² as aspen leaves (PETERSON, unpub.) and at least 200 g (dry wt)/m² as understory vegetation (DENNIS 1970). Applying the PETERSON et al. (1970) calorific determination of 4720 cal/g (dry wt) for aspen leaves to the total litter input (approx. 500 g/m²) the total annual energy input would amount to 2360 Kcal/m². In the absence of reliable respiratory values for the enchytraeids of the aspen site, it is not possible to make an accurate assessment of their metabolic role. However, assuming that they have the same degree of metabolic efficiency as those quoted in O'CONNOR (1967) the average monthly biomass of 3 g/m² of enchytraeids cannot account for more than 2—3% of the total energy input to the aspen litter layer.

6. Summary · Zusammenfassung

Ecological studies on Enchytraeidae associated with a fen and an area of aspen woodland in the Kananaskis valley, Alberta, Canada, were made during 1968 and 1969. The area has a continental type of climate.

The following species of Enchytraeidae belonging to 7 genera were found. Except *Henlea nasuta*, all are new records for Canada: *Henlea nasuta*; *Henlea perpusilla*, *Marionina argentae*; *Marionina craggi*; *Enchytraeus buchholzi*; *Fridericia bulboides*; *Mesenchytraeus armatus kananaskis*; *Cernosvitoviella christenseni*; *Marionina canadensis*; *Bryodrilus parvus kananaskis*.

Field experiments on the vertical movement of enchytraeids in relation to rising soil temperature and laboratory experiments on vertical movement in relation to moisture showed that enchytraeids moved downwards against rising soil temperature and decreasing humidity but movement was confined to the top 5 cm of the profile.

The O'Connor (1957) wet funnel technique was used to extract enchytraeids from soil cores for the determination of population densities. The Enchytraeidae on the aspen site showed two periods of high density, one in spring and the other in autumn with low densities in summer and winter. The maximum density recorded was 21,000/m^2 and the minimum density was 1900/m^2. The permanently moist fen soil showed only one period of high density in late summer or early autumn with the lowest density occurring in winter. The maximum density for the fen site was 10000/m^2 and the minimum was 500/m^2.

A significant positive correlation (at 5% level) between soil moisture and number of enchytraeids was found for the aspen site but not for the fen site. Soil temperature and the number of enchytraeids showed a significant positive correlation (at 5% level) in the fen site. Temperature and soil moisture were shown to be important factors for regulating the seasonal trend of enchytraeid populations.

The average standing crop (wet wt) of worms was 3 g/m^2 in the aspen study site and 0.5 g/m^2 in the fen study site. From calculations on the observed population turnover, production must exceed 3 × the average standing crop.

It is unlikely that the total energy utilized by the enchytraeids in the aspen site exceeded 2–3% of the total annual energy input (2360 Kcal/m^2).

Ökologie von Enchytraeiden in Böden der Rocky Mountains

Während der Jahre 1968 und 1969 wurden in einem Moor und einem Espenbestand im Kananaskis-Tal, Alberta, Kanada, ökologische Studien am Enchytraeiden-Besatz des Bodens durchgeführt. Die folgenden Enchytraeiden-Arten gehören zu 7 Gattungen (mit Ausnahme von *Henlea nasuta* sind alle Funde neu für Kanada): *Henlea nasuta*, *H. perpusilla*, *Marionina argentea*, *M. craggi*, *Enchytraeus buchholzi*, *Fridericia bulboides*, *Mesenchytraeus armatus kananaskis*, *Cernosvitoviella christenseni*, *Marionina canadensis* und *Bryodrilus parvus kananaskis*.

Freilandexperimente zur Untersuchung der temperaturbedingten Vertikalwanderungen von Enchytraeiden und Laborexperimente zur Untersuchung der feuchtigkeitsbedingten Vertikalwanderungen zeigten, daß Enchytraeiden gegen die ansteigende Temperatur und die abnehmende Feuchtigkeit nach unten abwandern, aber diese Ortsveränderungen waren auf die obersten 5 cm des Profils beschränkt.

Die Naß-Trichter-Technik von O'Connor (1957) wurde verwendet, um die Enchytraeiden zur Ermittlung ihrer Besatzdichte aus den Bodenproben zu extrahieren. Die Enchytraeiden des Espenbestandes zeigten zwei Perioden einer hohen Besatzdichte; eine im Frühjahr und die andere im Herbst, mit geringer Besatzdichte im Sommer und im Winter. Die höchste Besatzdichte betrug 21000 Ex./m^2 die niedrigste 1900 Ex./m^2. Der andauernd feuchte Moorboden zeigte lediglich eine Periode mit hoher Besatzdichte im Spätsommer oder Vorfrühling, mit der niedrigsten Besatzdichte im Winter. Die höchste Besatzdichte im Moor betrug 10000 Ex./m^2 und die niedrigste 500 Ex./m^2.

Eine signifikant positive Korrelation (bei 5% Irrtumswahrscheinlichkeit) zwischen Bodenfeuchtigkeit und Besatzdichte der Enchytraeiden wurde für den Espenbestand, nicht für das Moor ermittelt. Bodentemperatur und Besatzdichte der Enchytraeiden zeigten eine positive Korrelation (bei 5%) im Espenbestand. Temperatur und Bodenfeuchtigkeit erwiesen sich als bedeutende Faktoren für die Regulierung des jahreszeitlichen Trends des Massenwechsels der Enchytraeiden.

Die durchschittliche Biomasse („standig crop"; Lebendgewicht) der Enchytraeiden betrug 3 g/m^2 im Espen-Untersuchungsgebiet und 0,5 g/m^2 im Moor-Gebiet.

Auf Grund von Schätzungen des beobachteten Massenwechsels muß die Produktion etwa die 3fache Biomasse überschreiten. Es ist unwahrscheinlich, daß die totale Energie, die von Enchytraeiden im Espenbestand genutzt wird, 2–3% des totalen jährlichen Energie-Inputs (2360 Kcal/m^2) überschreitet.

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